First fossil mesothele spider, from the Carboniferous of France

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First fossil mesothele spider, from the Carboniferous of France. - *Eothele montceauensis* n. gen., n. sp., is described from two specimens from the Upper Carboniferous (Stephanian) of Montceau-les-Mines, France, as the first fossil and oldest known mesothele spider. In addition to the plesiomorphies characteristic of mesotheles, the holotype of *Eothele* preserves one mesothele synapomorphy (deep, narrow sternum) and at least one autapomorphy of the genus (biserially dentate chelicerae). The fossil is evidence that both mesotheles and opisthotheles were present in the Carboniferous period.

Key-words: Araneae - Carboniferous - fossil - France - Mesothelae - palaeontology - phylogeny.

INTRODUCTION

The south-east Asian spiders *Liphistius* Schiödte, 1849, and *Heptathela* Kishida, 1923, constitute the suborder Mesothelae which is sister group to Opistho-thelae to which all other extant spiders belong (PLATNICK & GERTSCH 1976). Meso-theles exhibit the most primitive character states of all living spiders, including segmented opisthosoma, eight spinnerets (seven in *Heptathela*) in a medioventral position on the opisthosoma, and absence of spinneret tartipores (SELDEN et al. 1991). Autapomorphies of Mesothelae include: modified trichobothria, invaginated fourth coxae, pseudosegmented lateral spinnerets, tibial spurs, and deep and narrow sternum (PLATNICK & GOLOBOFF 1985; RAVEN 1985). As primitive spiders, it would be expected that mesotheles should appear early in the fossil record and, indeed, many Carboniferous spiders were referred to this suborder (as Liphistiina) in the Treatise (PETRUNKEVITCH 1955). However, re-examination of all available types of

Carboniferous spiders for a monograph of the group (in preparation) has revealed that none shows autapomorphic characters of Mesothelae. Of the eleven genera included in Mesothelae in PETRUNKEVITCH (1955), one (*Palaeocteniza*) has been shown not to be a spider (SELDEN *et al.* 1991), and the remainder can be referred to Araneae only on the absence of autapomorphies of related orders (they have the general appearance of spiders, show segmented opisthosomae, but supposed spinnerets are artefacts).

In the last few years, some new specimens of fossil arachnids have been discovered at the locality known as Montceau-les-Mines in the Massif Central region of France. Among them, two specimens of Araneae have been identified, one of which is quite remarkable in that spinnerets are clearly preserved. The two specimens were mentioned briefly by SELDEN (1996) and are described fully here. The fossils are presumed to belong to the same species of spider, which shares most of the plesiomorphic character states of modern mesotheles, and a single synapomorphy: narrow, deep sternum (RAVEN 1985). At least one autapomorphy (biserial cheliceral dentition) separates the fossil species from living mesotheles. The fossil is evidence that both mesotheles and opisthotheles were present in the Carboniferous period.

MATERIAL AND METHODS

A number of fossil arachnids, including opilionids and trigonotarbids, are known from the Carboniferous (Stephanian) locality of Montceau-les-Mines in the Massif Central region of France, most of which are yet to be described. A recent review of the geology and palaeontology of the locality is given in HEYLER & POPLIN (1994). In that book, two photographs (p. 165) are labelled as spiders; the left photograph could be of a spider, but the specimen needs further development (specimen n° 5190/1), the other (specimen n° 6165) is not a spider. The specimen described here with the prefix 'In' is housed in the Department of Palaeontology, British Museum (Natural History), London, the other specimen is deposited in the Museum d'Histoire Naturelle, Autun, France. The fossils are external moulds in clay ironstone nodules.

THE MONTCEAU-LES-MINES SPIDER

Order ARANEAE Clerck, 1757
Suborder MESOTHELAE Pocock, 1892
Eothele n. gen.

Etymology: Greek *eos*, the dawn, and *thele*, a nipple; combining reference to the early age of the spider and the common suffix for mesotheles and mygalomorphs.

Diagnosis: mesothele spider with biserially dentate chelicerae ($\geq$ 5 teeth on promargin, $\geq$ 3 teeth on retromargin); at least 6 spinnerets in two rows (4, 2) on ventral surface of opisthosoma, not bunched together at posterior margin of second operculum.

Type and only species: *Eothele montceauensis* n. sp., described below.

Eothele montceauensis n. sp. (Figs 1–4)

Etymology: after Montceau-les-Mines, France, the provenance of the fossils.

Diagnosis: as for the genus.

Horizon & locality: Carboniferous (Stephanian), Montceau-les-Mines, Massif Central, France.

Type material: Holotype specimen, numbers 51961 (part) and 51962 (counter-part), housed in Museum d'Histoire Naturelle, Autun, France. Second specimen (not to be considered a paratype), In 62050 (part) and In 62050a (counterpart), same locality, British Museum (Natural History), London.

DESCRIPTION OF SPECIMEN 51961/2

The specimen consists of ventrolateral (part: specimen n° 51961) and dorso-lateral (counterpart: specimen n° 51962) external moulds in a nodule. The part shows most detail (Figs 1,3), including most of the prosoma and opisthosoma. The counter-part preserves only a few holes where legs disappear into the matrix, and vague details of the carapace. The dorsolateral mould of the opisthosoma, which should be on the counterpart, is missing; it is possible that a sliver of matrix preserving the mould was lost on splitting the nodule. It is impossible to tell whether the fossil represents a male, female or juvenile specimen.

The morphology of the specimen is essentially clear on the part (Figs 1,3). The opisthosoma has been compressed, the prosoma less so. The inflated shape of the opisthosoma indicates that this specimen represents a dead animal rather than a moult because in spider moults the opisthosoma is shrivelled. The coxae of all prosomal appendages on the left side, both chelicerae, and coxae of the right pedipalp and leg I are clearly displayed. The prosoma is tilted to the left, so that the coxae of legs II to IV are not seen on the part. Between the coxae, the labium and the left two-thirds of the sternum can be seen. The edge of the sternum drops steeply then flattens sharply to the right. The external mould of the labium disappears beneath the internal mould of the mouth. Labium and sternum are about the same width. Tilting the specimen reveals the external mould of the chelicerae (inset B on Fig. 3). Each of these shows a large pit distally which represents the external mould of the fang, and a line of holes (5 can be seen on each chelicera) running proximally from the fang represents the promarginal line of teeth. On the left chelicera, a line of three holes on the left side marks a retromarginal tooth row, but this cannot be matched on the right chelicera. Beyond the lateral edges of the coxae is a narrow groove which marks the external mould of the edge of the carapace. Beyond this there are some holes, the posterior two of which were developed further. These holes represent the external moulds of prosomal appendages. The posterior two represent the femora and patella of legs III and IV; looking inside the mould of femur IV, two grooves can be seen, which were ridges on the inferior surface of the femur in life. Two elongate holes about 4 mm from the edge of the carapace are two distal podomeres of leg I (presumably leg II is entirely hidden within the matrix). A small hole close to the carapace edge is the

FIGS 1 & 2

Eothele montceauensis n. gen., n. sp., Carboniferous (Stephanian), Montceau-les-Mines, France. Fig. 1 (upper): holotype, specimen 51961 (part); see Fig. 3 for explanation; x13. Fig. 2 (lower): additional specimen, In 62050 (part); see Fig. 4 for explanation; x6.
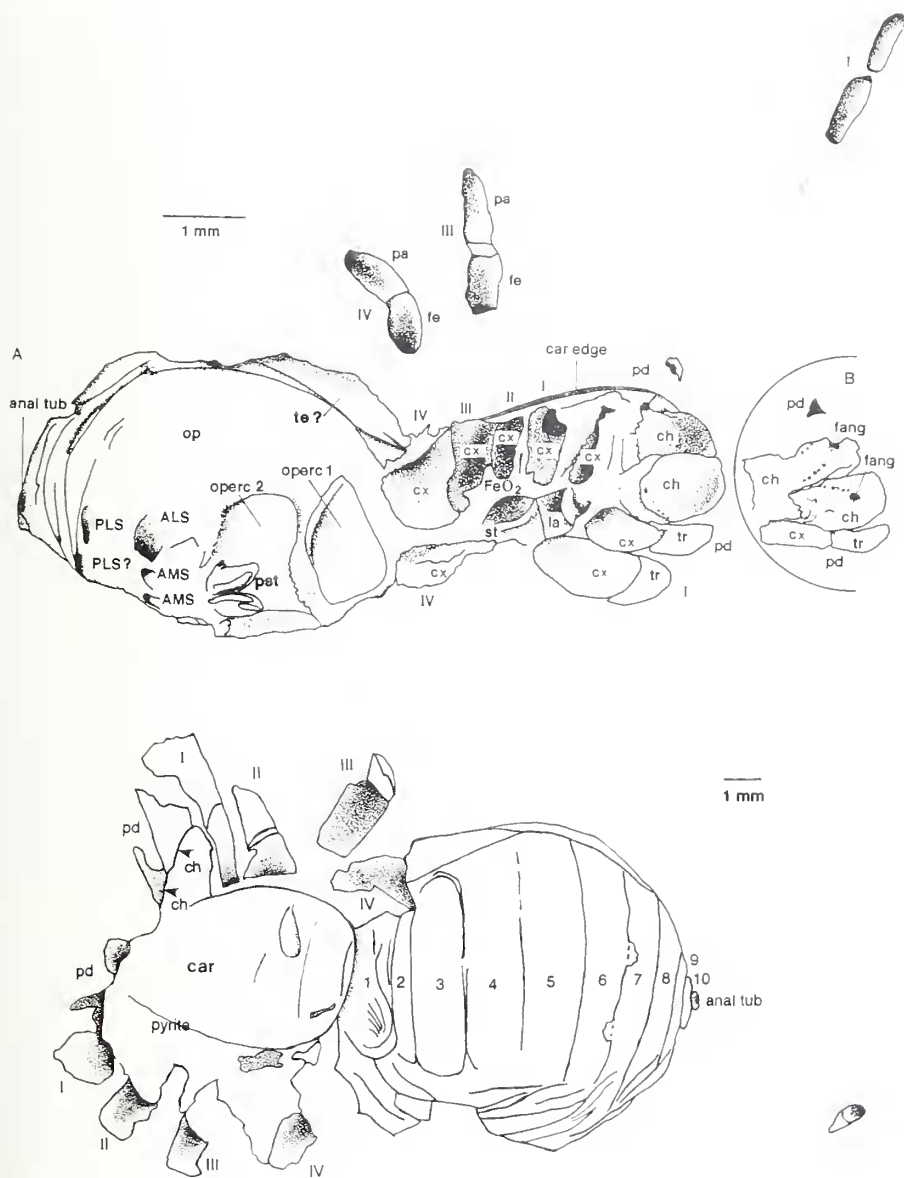
FIGS 3 & 4. *Eothele montceauensis* n. gen., n. sp., Carboniferous (Stephanian), Montceau-les-Mines, France. Fig. 3 (upper): holotype, specimen 51961 (part); A: right dorsolateral view of external mould of left ventrolateral; B: dorsal view of external mould of chelicerae showing fangs (holes disappearing into matrix) and tooth rows. Fig. 4 (lower): additional specimen, In 62050 (part), ventral view of external mould of dorsal. Legend for Figs 3 & 4: 1–10—opisthosomal tergite numbers, ALS—anterior lateral spinneret, AMS—anterior median spinneret, anal tub—anal tubercle, car—carapace, ch—chelicera, cx—coxa, fe—femur, I–IV—walking legs I–IV, la—labium, operc—book-lung operculum, op—opisthosoma, pa—patella, pd—pedipalp, PLS—posterior lateral spinneret, pst—paired structure, st—sternum, te—tergite, tr—trochanter.

mould of the left pedipalp; it lines up with a hole in the counterpart. The region of leg II to IV coxae is obscure; whilst some shapes can be made out, it is not obvious whether they represent the mesial edges of coxae or also include any additional sternites. The counterpart shows small holes which represent the femora of right legs IV, III and II. The external mould of femur 1 is clearly displayed, disappearing into the matrix, with the mould of the pedipalp femur in front. On the other side, the left pedipalp femur mould can be seen. If the specimen is tilted so that the area to the mesial side of the legs is flat, a symmetrical shape can be discerned, which represents the external mould of the anterior part of the carapace in the eye region. Some circular structures can be made out, but they are rather faint. No trace of the opisthosoma is seen on the counterpart.

The opisthosoma on the part is beautifully displayed, and larger than the prosoma. It shows, on the right side in the anterior half, two sternites (book-lung opercula). The left lateral and median parts of these are flat, but their right sides bend upwards and are folded at the edge of the specimen. The anterior sternite has a straight anterior edge, the lateral edge runs obliquely inwards then curves to form the posterior edge which parallels the anterior. The second operculum is slightly larger than the first, and has procurved anterior and posterior margins and rounded lateral margins. In a posteromedial position on the second operculum is a pair of subelliptical areas of internal mould, which represent paired internal sac-like structures lying above the second operculum and opening to the medial part of its posterior border in life. These were initially interpreted as paired receptacula of the female vulva, but in living spiders the genitalia are on the second opisthosomal somite; the second oper-culum is on the third opisthosomal somite. In the fossil, the book-lung opercula are interpreted as belonging to somites 2 and 3, as in *Liphistius*. These sac-like structures are most similar to the supposed tracheal organs of the mesothele *Heptathela* (YOSHIKURA 1954); they do not occur in *Liphistius*, but may be homologous to the eversible sacs in Amblypygi (KAESTNER 1968).

Posterior to the second operculum are three holes extending into the matrix, the leftmost being larger than the other two, which are about the same size. These are interpreted as external moulds of the left anterior lateral spinneret (ALS) and the anterior median spinneret pair (AMS). The right ALS is presumed lost among the folds of the right part of the opisthosoma in the fossil. Posterior to the anterior spin-neret moulds are two more holes which represent posterior spinnerets. The anterior spinnerets are in the mesothele conformation. Four posterior spinnerets (smaller posterior median, PMS; larger posterior lateral, PLS) are present in all spiders, except when the PMS are missing (some specialized mygalomorphs and araneomorphs), or a single PMS is present (the mesothele *Heptathela*). The fossil posterior spinnerets could represent left PLS and left PMS, PLS only, PMS only, or left PLS and single PMS. Evidence favouring a single pair of posterior spinnerets is a) the holes are approximately the same size, and b) an imaginary midventral line running from between the paired median structures of the second operculum, between the AMS, to the anal tubercle, parallel to the edge of the opisthosoma would pass between the two holes, but a line passing to the right of the right-most hole would have to follow a

dog-leg course to reach the anal tubercle. Since the PMS are usually smaller than the PLS, or lost (Marples, 1967), the posterior spinnerets present in the fossil, which are relatively large, are most probably PLS.

The left side of the opisthosoma bears a number of random, irregular nodules. Beyond these are some curved folds which approximately parallel the edge of the opisthosoma. No tergites are visible. This may be because any tergites which were present were confined to the dorsal side of the opisthosoma. On the part, only ventral and lateral sides are visible, the counterpart preserves no fragment of the opisthosoma. On the left lateral side of the opisthosoma, which would have been the anterior part of the dorsolateral in life, one fold is larger and more robust than the rest (which suggests it was composed of tougher cuticle in life) and extends for about 1/3 of the length of the opisthosoma. In front of this structure is a smaller, yet similarly robust fold. The possibility that the larger structure could represent a dorsal scutum was considered, but further thought and study of some other well-preserved Carboniferous spiders has led to the conclusion that this specimen probably did bear dorsal tergites. These, like the carapace, would have been preserved on the counterpart. However, like the carapace, which is preserved on the part as a thin groove—the external mould of the edge of the carapace, the opisthosomal tergites have also left their mark on the part as a narrow external mould. I suggest that during compression of the fossil, the dorsal tergites remained fairly rigid compared to the flexible cuticle of the sides of the opisthosoma. Where there were no adjacent tergites, such as over most of the preserved left and posterior parts of the opisthosoma, this flexible cuticle is expressed as simple folds on the external mould. On the left anterolateral side, however, the second and following tergites above compressed the flexible cuticle onto the sediment to produce an apparently robust fold. In front of this, the short first opisthosomal tergite has produced a similar fold. Segmentation is not apparent because it is the lateral cuticle which formed the floor of the crevice, not the tergites themselves.

DESCRIPTION OF SPECIMEN IN 62050

The specimen (Figs 2,4) consists of dorsal (part: specimen n° 62050) and ventral (counterpart: specimen n° 62050a) external moulds in a nodule. The part shows most detail (Figs 2,4), including much of the prosoma and dorsal opisthosoma. The counterpart preserves only a few holes where legs disappear into the matrix, and some parts of the book-lung opercula on the ventral opisthosoma. The ventral mould of the prosoma, which should be on the counterpart, is missing because a sliver of matrix preserving the mould was lost on splitting the nodule. In places, details are obscured by a thin veneer of pyrite and calcite (?) crystals; kaolinite is rare, and occurs mainly as a cast of thin tubes (possibly distal podomeres) towards the edge of the nodule. The specimen is strongly three-dimensional, its shape no doubt reflects the original shape of the animal. There is slight distortion in that the prosoma is rotated slightly in relation to the opisthosoma, so that in the chelicerae and other prosomal appendages appear to lie off the midline of the carapace when the specimen is lying with the opisthosoma symmetrical to view. By rotating the specimen, the

carapace and appendages can be positioned so that they are almost symmetrical, when the opisthosoma is not. The slight displacement of the chelicerae is then explained by a little compaction of the sediment prior to the formation of the nodule. It is impossible to tell whether the fossil represents a male, female or juvenile specimen.

The carapace is preserved as an external mould, but is obscured, especially anteriorly, by mineralisation. It is roughly oval in shape, widest at or behind its midlength, but the anterior border is not visible in the specimen, being covered by matrix surrounding the anterior appendages. The posterior margin of the carapace is approximately straight, with a slightly recurved submarginal line; it is about half the width of the carapace at its widest. The chelicerae are preserved as two holes, separated by a mineralised sheet of rock matrix, anterior to the carapace and disappearing into the nodule anteriorly. No details can be discerned. The pedipalps and walking legs are preserved only as external moulds of parts of the proximal podomeres. Holes descending into the matrix around the carapace represent the upwardly rising femora. A few thin holes well beyond the main body of the fossil may represent distal podomeres descending again.

The opisthosoma is represented on the part by a sub-hemispherical hole: the external mould of its three-dimensional form. The inflated shape of the opisthosoma indicates that this specimen represents a dead animal rather than a moult because in spider moults the opisthosoma is shrivelled. Lateral parts of the opisthosoma, especially anteriorly, are distinctively longitudinally wrinkled. (Similar wrinkling occurs on the soft parts of the opisthosoma of *Liphistius*). The dorsal surface of the opisthosoma consists of a series of tergites, at least eight can be counted. The more anterior tergites are longer (sag.) than the posterior, but telescoping of the opisthosoma posteriorly conceals their true lengths. Another tergite (1) may be present between the most anterior well-defined tergite and the carapace, but wrinkling on the left side of the specimen (right side of the animal) suggests that this area could consist of soft cuticle. The tergites have fairly straight anterior and posterior margins and, where visible, their lateral margins appear to be rounded. At the posterior end of the opisthosoma, just posterior to a possible microtergite (10), is a hole which represents the external mould of the anal tubercle. On the counterpart (specimen n° 62050a), the external mould of a small part of the left side of the opisthosoma can be seen. This region is characteristically transversely wrinkled. Two transverse grooves may represent the posterior margins of book-lung opercula 1 and 2.

DISCUSSION

It is tempting to assume that the two Montceau specimens belong to the same species, but the morphological evidence neither proves nor disproves this supposition. Features shown by the Autun specimen are not preserved on the London specimen, and vice versa. However, the two fossils are approximately the same size and occur in the same locality and lithology. At other Upper Carboniferous localities yielding arachnids in concretions, such as Coseley (UK) and Nýřany (Czech Republic), diversity within orders is low, and similar specimens have usually been assigned to

the same species (this is true for the Nýřany 'spiders', but is not yet published). All ten specimens of the earliest mygalomorph, *Rosamygale grauvogeli* Selden & Gall, 1992, found at the Triassic locality in the Vosges, France, belonged to one species. For these reasons, the two Montceau-les-Mines specimens will be assumed to be conspecific, until further evidence (in the form of more specimens) might prove otherwise.

Since the two specimens reveal essentially different aspects of the morphology of the Montceau spider, a reasonable reconstruction of the living animal can be built up. The fossil animal is clearly a spider because of the presence of spinnerets (at least, appendages are present in the position in which spinnerets occur in living spiders, and no other arachnid has such appendages in this position; spinnerets are taken to indicate the presence of opisthosomal silk glands) combined with a pedicel, an essentially flexible opisthosoma with the tergites 'floating' in softer cuticle, general appearance of the carapace and sternum, and lack of autapomorphies of other arachnid groups. Some autapomorphies of spiders, naked fang and cheliceral poison gland for example (SELDEN *et al.* 1991), cannot be seen.

There are few described autapomorphies of mesotheles (PLATNICK & GERTSCH 1976; PLATNICK & GOLOBOFF 1985). One of these relates to chromosome numbers so cannot be confirmed in fossils; the other characters (trichobothrial bases, invaginations of fourth coxae, multisegmented lateral spinnerets, tibial spurs) are morphological, but none of them can be seen in the Montceau fossils. An additional apomorphy of mesotheles was suggested by RAVEN (1985): a deep and narrow sternum. He contended that the presence of a sternum is an autapomorphy of Araneae (it is absent or very small in Amblypygi and most other arachnids), and that in Opisthothelae it is wide and low (an autapomorphy of that group). SELDEN *et al.* (1991) considered the presence of a sternum to be plesiomorphic within the Tetrapulmonata (Trigonotarbida have one also), but this does not alter the apomorphic state of the sternum in the mesotheles and opisthotheles. The characters of dorsal opisthosomal tergites, two ventral opercula (covering the two pairs of book-lungs), orthognath chelicerae, and AMS fully developed, are all indicative of Mesothelae, but are plesiomorphies. The deep, narrow sternum of the Montceau spider is a character shared with modern mesotheles. If the paired structures above the second operculum in the fossil are not homologous with amblypygid eversible sacs then this character would be a synapomorphy for *Heptathela* and *Eothele* n. gen. (Fig. 5A). The spinneret pairs in *Eothele* are widely spaced between the second operculum and the anal tubercle, not bunched together just behind the second operculum as in modern mesotheles nor close to the anal tubercle as in Opisthothelae. The position of the spinnerets in *Eothele* could reflect the start of their rearward movement towards the opisthothelate condition, or a more ancestral arrangement prior to the bunching of the spinnerets close to the second operculum as seen in *Liphistius*. If the posterior spinnerets in *Eothele* are really PLS, then it would represent a new configuration for Araneae, an advance over the *Heptathela* condition (with a single PMS), and an autapomorphy for the fossil species. Another feature which separates *Eothele* from modern mesotheles is the presence in the fossil of two rows of teeth on the chelicera (Fig. 3,B); only a

promarginal row is present in living forms (ABRAHAM 1929; BRISTOWE 1932). Bise-rially dentate chelicerae are special adaptations which have evolved in a number of spider groups. For example, RAVEN (1985) considered the biserial condition to be apomorphic in ctenizoid mygalomorphs and some related idiopids and cyrtaucheniids. Amblypygids and the Devonian spider *Attercopus* have uniserially dentate chelicerae (SELDEN *et al.* 1991).

FOSSILS AND PHYLOGENY

Much has been written concerning the value of fossils in piecing together the relationships between animal groups (see a recent review by SMITH, 1994). It has become clear in the last twenty years or so that fossils must play a secondary role in establishing phylogenetic relationships, but an important one in providing raw data and, in some cases, resolving conflicting cladograms. Some authors have attempted to use stratigraphic data in cladistic analyses (e.g. FISHER 1992, 1994; WAGNER 1995) but such analyses need to be executed with caution. The fossil record of arachnids is still so sparse that the discovery of single specimens can make major alterations to the known fossil record. The new spider described here is a case in point: it is the first known fossil mesothele, thus extending the record of this group from 0 years to 290 million years. The unique contribution fossils can make is in the construction of evolutionary trees, the next logical step in understanding the phylogenetic history of an animal group after the construction of cladograms. It has been shown (for example by SMITH 1994, chapter 6) that stratigraphic data can be combined with a robust cladogram to produce an estimate of the evolutionary tree of a group which minimises stratigraphic gaps. A normal result of this process is the production of range exten-sions and ghost lineages; these are predictions made by the data. Note that fossil data provides minimum estimates for the dates of divergence of clades.

Possession of many character states which indicate that the Montceau spider is plesiomorphic with respect to Opisthothelae, and one character state (sternum narrow and deep) which is an autapomorphy of Mesothelae, confirm that the Montceau spider belongs in Mesothelae. The fossil species cannot be ancestral to any modern meso-thele because of at least one autapomorphy (biserially dentate chelicera). Therefore, the fossil is the oldest record of a mesothele. Furthermore, since Opisthothelae (Mygalomorphae + Araneomorphae) is the sister clade to Mesothelae, it must have originated sometime prior to the age of the fossil. Fig. 5 illustrates these relationships.
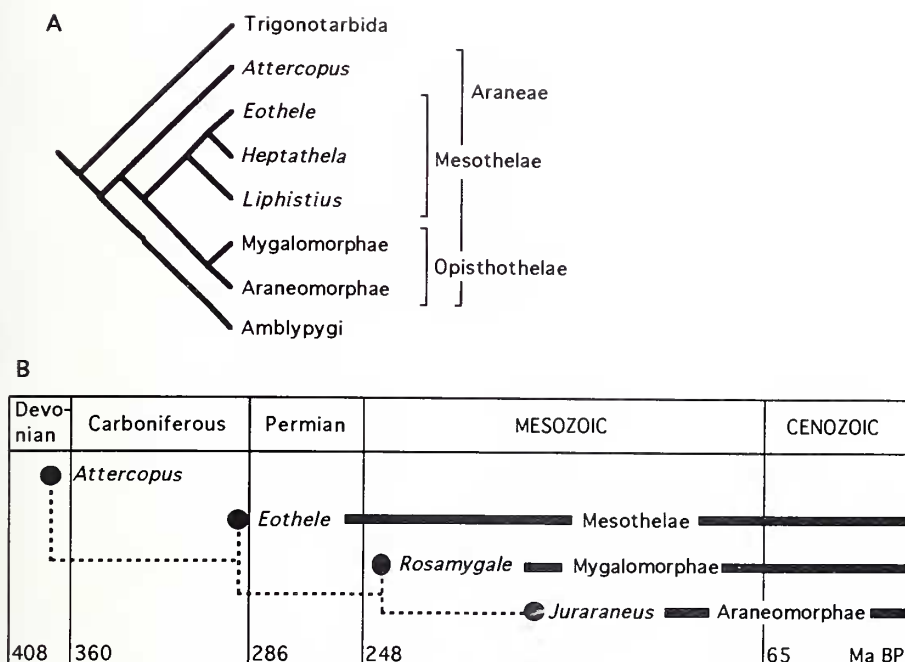
Fig. 5

A: cladogram of relationships among Trigonotarbida, Amblypygi, and selected spider taxa. The Montceau spider *Eothele* is shown as sister to *Heptathela* because tracheal sacs are absent in *Liphistius* and on the assumption that PMS are lost in *Eothele*. B: Evolutionary tree showing relationships between spider suborders (emphasising the earliest fossil members) and *Attercopus*; solid black lines are known ranges (fossil record of Mesothelae consists solely of *Eothele*; other suborders have better fossil records); horizontal dashed lines are ghost lineages for (Mesothelae + Opisthothelae) and (Mygalomorphae + Araneomorphae) and range extension for Araneomorphae; vertical dashed lines show hypothesized relationships.

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